## 248 Mr. J. W. Howell on the Structure of the Capsule

Some of these questions comprise several others. To solve them two things only are necessary, accuracy and perseverance. M. Vaucher has afforded us an example of both these qualities. His history of the *Confervæ* is remarkable for its precision in the explanation of new and delicate facts. His last work required the average duration of man's life, and we may say, in general, that during sixty years M. Vaucher rarely turned aside from botany. From it he derived lively gratification; the result of his works has enriched the science; let us hope that others may endeavour to imitate him, and let us ever religiously preserve the memory of a philosopher so well entitled to our respectful recollection. ALPH. DEC.

XXXVI.—On some hitherto unnoticed peculiarities in the Structure of the Capsule of Papaveraceæ; and on the Nature of the Stigma of Cruciferæ. By J. W. HOWELL, Esq., M.R.C.S.

THE capsule of *Papaver* apparently bears so close a resemblance to that of *Nymphæa*, that it forms one of DeCandolle's reasons for considering the *Papaveraceæ* and *Nymphæaceæ* to be allied\*. The capsule in each genus is syncarpous, with ovuliferous dissepiments, and is crowned with a many-rayed stigma, the number of rays corresponding to that of the dissepiments. The chief structural difference hitherto observed between these capsules consists in that of *Nymphæa* being composed of several carpels surrounding the axis, and having the dissepiments formed by the juxtaposition of the ovuliferous sides of the perfect cells with intermediate plates of connecting cellular tissue; whilst in *Papaver* the inflected sides of the conjoined carpels not being continued to the axis, the imperfect ovuliferous dissepiments project only midway into the cavity of the capsule, and thus leave it one-celled.

On a more attentive examination, however, a difference will

\* "Ob structuram fructus et stigmatis *Papaveri* valde similem."-Regni Veget. Syst. Nat. vol. ii. p. 42.

This similarity of structure is repeatedly alluded to by this author; thus, in "Nymphæaceæ—Styli \* \* \* connati stigmatibus supra urceolum peltatim (exacté ut in Papavere) radiatis basi connatis apice liberis," vol. ii. p. 39. Again: "\* \* \* structura fructus Papaveris parum recedit a vera Nupharis structura," p. 43. Again: "Papaveraccæ accedunt hinc mediante Papavere ad Nymphæaceas," p. 68.

In 'Flore Franc.,' DeCandelle included Nymphæa and its immediately allied genera in Papaveraceæ, in which this great botanist followed the example of Linnæus, who had previously referred Nymphæa to his twentyseventh Order, Rhæadeæ, which very nearly corresponds with the Papaveraceæ of modern authors. be detected, which has never to my knowledge been noticed. This difference will be found of very considerable interest and importance, from its affording an apparent exception to a general law of great value in systematic botany, and from the assistance which, when rightly understood, it is capable of affording in the elucidation of other obscure and apparently anomalous forms of structure. The peculiarity to which I allude consists in the difference of the relation which the stigmatic rays bear to the dissepiments in the capsules of the Nymphæaceæ and in the Papaveraceæ. In the Nymphæaceæ the stigmatic rays alternate with the ovuliferous dissepiments, in correspondence with the law (hitherto considered intact), that "parietal placentæ must alternate with the stigmas;" whilst in Papaveraceæ the stigmatic rays are opposite to the dissepiments! This important differential character, which I detected in 1832, appears not even at this time to be known to those systematists who have written on the natural orders of plants; at least it is not mentioned by Jussieu, 'Tab. du Règne Vég.,' par Vent.; Smith, 'Eng. Flora;' DeCandolle, 'Syst. Nat.' and 'Prodromus;' S. F. Gray, 'Nat. Arrang. Brit. Pl.;' Salisbury, who established the Order Nymphæaceæ in 'Annals Bot.;' Lindley, 'Int. Nat. Syst.' and 'Synopsis Brit. Fl.;' Burnett, 'Outlines to Bot.;' Don, 'Gen. Syst. Bot.;' Royle, 'Bot. of Himalayas;' Hooker, 'Bot. Mag.' arranged according to natural orders; nor Drs. Torrey and Asa Gray, 'Flora of North America,' 1840, which is the latest published systematic work. Indeed, so entirely unaware are even the latest of these writers of the existence of this character, as a differential one, serving to separate by abruptly defined limits those otherwise nearly allied orders, that Lindley, Hooker, and the authors of the 'Flora of North America,' in describing the relation of the dissepiments to the stigmas in Papaveraceæ, in which alone they notice it, describe it wrongly; the first two writers entirely so, and the latter in part! Dr. Lindley says, "stigmas alternate with the placentas" (!), which Drs. Torrey and Asa Gray repeat, excepting only Papaver itself, in which they correctly say they are "opposite," and Meconopsis, which they distinguish by a mark of doubt (?).

There seem to be but two possible modes of accounting for this apparent anomaly in the *Papaveraceæ*:—first, that the seminiferous dissepiments are not true placentas formed by the adhesion of the inflected sides of contiguous carpels (which would appear to necessitate their *alternation* with the stigmas), but are merely projections of cellular tissue forming seminiferous plates extending into the cavity of the capsule, and proceeding from the centre of the internal face of cach of the carpellary valves. The assumption, however, that ovules may be

#### 250 Mr. J. W. Howell on the Structure of the Capsule

generated upon the *centre* of the face of the carpellary valves, is opposed to all that is certainly known upon the subject. Even in those cases in which the ovules are indeed borne on a great portion of the inner face of the carpel, the centre is entirely destitute of them, as in *Limnocharis*. The first supposition, therefore, based on this untenable assumption, cannot be entertained; in fact, it is only mentioned to show the greater necessity for receiving the remaining mode of explanation, notwithstanding its apparent paradoxical nature, viz. that the seminiferous dissepiments are true parietal placentas, but that *each stigmatic ray is double,—formed of the adjacent lateral portions of the stigmas of two contiguous carpels; the two portions of the stigma of each carpel in the more complex capsules* of the higher species being separated by an intervening membrane ! Ex. Argemone, Papaver.

It is obvious that nothing less than the most rigorous demonstration will suffice to establish so remarkable a mode of explanation, and this can only be effected by tracing the successive steps of gradually increasing elaboration of the capsule, from its most simple condition in *Bocconia*, through *Macleaya*, *Chelidonium*, *Glaucium*, *Hunnemannia*, *Eschcholtzia*, *Meconopsis* and *Argemone*, to the state of greatest complexity in *Papaver somniferum*. Notwithstanding the great difference in the forms and appearances of the capsules of these genera, they exhibit a perfect similarity in all *essential* particulars of their structure, their differences being dependent, not on the relative disposition of their constituent parts, but on their proportion, magnitude, and number.

The simplest state of the capsule in the Papaveraceæ is exhibited by Bocconia, Linn., in which it consists of two dorsally-compressed carpels united by their margins, forming a flattened one-celled capsule containing a single seed, which is attached to the inferior part of the replum or annular receptacle formed by the united margins of the carpels, from which the greater portion of the latter separates in the form of valves. This annular receptacle is shown to be identical with true parietal placentas, although, except at a single point at its base, it does not bear ovules, by the latter being developed throughout its entire vertical extent on both sides the capsule in the cognate species, Macleaya cordata, Brown (Bocconia cordata, Linn.). The capsule is crowned by a deeply bifid stigma, whose internally plumose halves being widely reflexed correspond in situation and direction to their subjacent valves, and therefore alternate with the intervalvular parietal placentas.

It is interesting to remark, that in this, the simplest state of the structure of the capsule, the relation of parts exemplifies the law which expresses the necessary *alternation* of stigmas

# of Papaveraceæ, and on the Stigma of Cruciferæ. 251

with parietal placentas; and that it is therefore the reverse of that exhibited by the more complex capsules.

In *Macleaya cordata* the two parietal placentas bear several ovules; and the lobes of the stigma, though capable of separation, are vertical and in close apposition, forming a furrowed stigmatic line, which necessarily *corresponds* to the placentas, and consequently *alternates* with the valves.

In *Chelidonium* the stigmatic lobes (which in *Macleaya* were capable of separation and complete reflexion) are more rigidly erect, but the furrowed line bears the same relation to the placentas, which now exhibit their bi-carpellary origin by bearing a double row of ovules.

In *Glaucium* the stigmatic lobes become enlarged, but otherwise remain as in the last example. The parietal placentas are furnished with a linear spongy growth projecting from between the rows of ovules of each placenta, and uniting with that of the opposite side in the centre of the capsule, which is thus converted into two cells. This spongy dissepiment is usually described as arising from the extension of the placentas; an attentive examination at different periods of growth, however, will show that it is really distinct in structure, though attached to them.

In *Hunnemannia* we have the first indication of an addition of parts; the stigma being obscurely four-lobed, indicating the manner in which new carpels will, in other genera, become interposed between the two primary ones, which alone exist in the preceding instances.

In *Eschscholtzia* the additional stigmas (which are only indicated in *Hunnemannia*) are considerably developed, but are separate from the primary ones. The fact of their being the superadded stigmas is however indicated by their being shorter than the others.

[In consequence of the separation of the stigmas in this genus, the primary or longer ones bear the normal relation to the placentas, i. e. alternate with them, as already described in *Bocconia*; and the superadded stigmas (the shorter ones), which are opposite to the placentas, are so only in consequence of the non-development of the carpels to which they really belong. It will be perceived, that whilst in this genus the approach towards a greater complexity of structure takes place in some organs, others appear to have retrograded towards the normal state as it is exhibited in *Bocconia*, the first instance in the series; thus, the increased development of the genus after *Hunnemannia*, and consequently after *Glaucium* and *Chelidonium*, is attended by the separation of all the stigmas, and the consequent alternation of the primary ones with the

## 252 Mr. J. W. Howell on the Structure of the Capsule

parietal placentas, which is the normal state. This co-existence of structural progression and retrogradation is not peculiar to the present case, but obtains in all kinds of organized beings, and effectually negatives any attempt at linear arrangements, either of individual organs or of species themselves.]

In *Meconopsis* the additional carpels (only sketched forth and indicated, as it were, by the additional stigmas in *Hunnemannia* and *Eschcholtzia*) are perfected, each carpellary valve contributing by its margins to the formation of two parietal linear placentas, which latter *correspond* with the stigmatic rays. Each stigmatic ray is formed precisely similar to the stigma of *Macleaya*, *Chelidonium* and *Glaucium*, being furnished with a central depressed line, indicating its formation from the union of the corresponding halves of the two contiguous carpels.

In Argemone the radiated stigma presents an undulatory folded appearance in consequence of the increased growth of the intervening tissue, which in the preceding genera (excepting Eschscholtzia) separates the lateral portions of the stigmatic extremity of each carpel.

[If the reader experience any difficulty in understanding the complicated folded stigma of *Argemone*, let him compare one of the folds with the stigma of *Glaucium*, and the difficulty immediately vanishes; for he will perceive that the undulated stigma of *Argemone* results merely from the structure of *Glaucium* being several times repeated, and arranged in a circular manner around an imaginary axis.]

We now arrive at *Papaver*, in the different species of which the capsule presents several states of complication by the successive addition of a greater number of carpels, which in *P. somniferum* sometimes amount to sixteen. The parietal placentas, which in all the preceding genera are linear, now project in towards the centre of the capsule, partially dividing it into as many imperfect cells. The stigmatic rays, which, as in the preceding instances, are equal in number to the placentas, and *opposite* to them, are, as already described, double, and only differ from those of *Argemone* in having the intervening tissue, which separates the two margins of the stigmatic extremity of each carpel, plane instead of folded.

We now see that the radiated stigma of *Papaver*, however much it may appear to resemble that of *Nymphæa*, differs from it in such important particulars as effectually to prevent any union of the two orders to which these genera belong; unless, indeed, species of *Nymphæaceæ* should hereafter be discovered with bi-carpellary capsules, which would form, with *Bocconia*, the means of union with *Papaveraceæ* at the commencement of the two series. What are the practical bearings of this anatomical peculiarity in the stigmas of *Papaveraceæ*? Observe the assistance it affords in elucidating the hitherto controverted structure of the stigma and capsule of *Cruciferæ*. In this order the variably elongated capsule consists of a single cell with two linear parietal placentas, each of these terminating superiorly in a stigma! The placentas are occasionally united by an intervening membrane, converting the capsule into two cells. When ripe the capsule separates into three parts—two lateral valves and an intervening replum, formed of the persistent parietal placentas, which are crowned by the two permanent stigmas !

Dr. Brown appears to have been the first to establish a general principle for explaining the structure of complex capsules; his words are, "Capsulas omnes pluriloculares e totidem thecis conferruminatas esse, diversas solum modis gradibusque variis cohæsionis et solubilitatis partium judico," 'Prod. Fl. Nov. Holl.,' p. 558, 1810. In 1818, 'Linn. Trans.,' he applied this principle to the explanation of the seed-vessel of the *Compositæ*, and showed its one-seeded achenium to be an extreme state of simplification of an organ arising from deprivation of parts, and to be in reality a bi-carpellary capsule, in which only a single seed is developed on one parietal placenta and none on the other—the parietal placentas being represented by two delicate cords; and referred also to Bocconia, as an analogous instance in Papaveracea ; and likewise to Proteaceæ, for other instances illustrative of the successively increasing imperfection which leads from the normal type to the most anomalous conditions. In 1821, DeCandolle, in a memoir on the Cruciferæ, 'Annales du Muséum,' and in the article on the same family in 'Systema Naturale,' described the capsule in strict conformity with the principles of Brown (without acknowledging himself indebted to the latter), as being composed of two carpels whose corresponding inflected margins formed the parietal placentas; the bi-carpellary origin of each placenta being indicated by its bearing a double row of ovules. See diagram of structure of the silique in DeCandolle's Memoir.] In 1826, Brown, in 'Appendix to Denham's Voyage,' p. 217, having substantiated his claim to priority of discovery of the bi-carpellary nature of the capsule of Cruciferæ, by referring to his observations of 1810 and 1818, as quoted above, and having absolved DeCandolle from any charge of plagiarism, further proved the double nature of the placentas and dissepiment, by showing that the two lamellæ of which the latter is composed are frequently separable, and that when this is not the case, the constituent lamellæ are rendered evident by the want of correspondence of their

### 254 Mr. J. W. Howell on the Capsule of Papaveraceæ, &c.

vascular areolæ. Thus far, then, the two highest botanical authorities agree in considering the silique to be composed of two carpels, and such is really the case,-but, as Lindley justly remarks, 'Int. Nat. Syst.,' ed. 1, " This does not remove the difficulty of the stigmata being opposite the placentas, instead of alternate with them." To meet this difficulty, DeCandolle (according to Lindley) proposed a theory, which, in addition to some untenable assumptions, included the supposition of each stigma being composed of two lateral halves, in a state of cohesion, each half being the continuation of the lamella of the placenta of the corresponding carpel. As, at the time this theory was proposed, the assumption here quoted was altogether gratuitous, there being no actually observed structures then known to corroborate it, Lindley (Op. cit. and 'Bot. Register,' fol. 1168 with diagrams) proposed another, founded on the structure of Eschscholtzia, wherein he concludes that the silique of Cruciferæ is formed of four carpels, instead of two; that the alternate ones are reduced in lateral extent, but have their placentas perfect; and that the stigmas of the silique belong to them, while the two remaining carpels have lost their placentas and stigmas, and are thus reduced to the form of valves. In this manner, the correspondence of the stigmas with the parietal placentas was shown not to be an exception to the law which expresses their necessary alternation, but to be in strict conformity with it, the correspondence of the stigmas and placentas being only apparent, not real. The object in forming this ingenious though complex theory was to avoid De-Candolle's hypothetical assumption of the compound nature of the stigma, which Lindley rejected, notwithstanding that Brown considered its truth to be rendered probable by the evidence of some monstrous varieties of the siliquose capsule. As, however, the admission of the compound structure of the stigma meets all the difficulties of the case, and explains the apparently anomalous arrangement of parts in an easy and concise manner, and as of two proposed theories we are warranted in selecting that which is most simple, I have much satisfaction in being the first to adduce proof, derived from actual structures, that the individual stigmas of syncarpous capsules are occasionally compounded of the adjacent lateral halves of contiguous carpels. Hence I conclude, with Brown and DeCandolle :---

1st. That it is most probable that the silique of *Cruciferæ* is composed of two carpels, whose inflected margins form two bi-lamellate parietal placentas; and that the apparently anomalous disposition of the stigmas arises from their being formed of two lateral halves, each of which belongs to the corresponding subjacent carpel.

2nd. That the alliance of the *Papaveraceæ* and *Brassicaceæ* (*Cruciferæ*) is, in respect of the structure of the capsule, more close than heretofore supposed; in illustration of which we find that the two-celled, many-seeded silique of *Glaucium* has its perfect analogue in that of *Brassica*, whilst the comparatively imperfect state of the one-celled, single-seeded silicule of *Isatis* in the second order, is represented in the first by the similarly-constructed capsule of *Bocconia*.

3rd. That the enunciation of the law which expresses the necessary alternation of stigmas with dissepiments (Lindley's 'Key to Structural Botany,' § 379.), and with parietal placentas, must be modified to embrace the above-described facts, and may be conveniently and correctly expressed thus: That in syncarpous capsules, parietal placentas, and therefore dissepiments, always alternate with simple stigmas formed by single carpels, but are opposite to those which are formed by the union of the adjacent margins of contiguous carpels.

Bath, 5 Axford's Buildings.

[Note.—In Kunth's 'Flora Berolinensis,' (published in 1838) we find (v. i. p. 29) the stigma of *Papaveraceæ* described as follows :—" Stigmata tot quot placentæ, cum his alternantia, magis minusvé connata, \*\*\* sinubus inter stigmata sæpe ampliatis lobosque referentibus cum stigmatibus alternantes (a plurimis pro his sumptos) placentisque oppositos." In the generic description of *Papaver* (p. 30) he says, " Stigma magnum, sessile, 5–20-lobum : lobi sursum inflexi, \*\*\* marginibus stigmaticis per paria contiguis radios formantes tot quot lobi, placentis oppositos; sinubus sæpe ampliatis inque lobos productis spurios, cum legitimis alternantes." No other description of this curious structure has come under our notice\*.—*Ed. Ann. Nat. Hist.*]

XXXVII.—Descriptions of some new Genera and fifty unrecorded Species of Mammalia. By J. E. GRAY, Esq., F.R.S.

MY DEAR SIR, British Museum, Oct. 10, 1842. I HAVE sent you for insertion in the 'Annals' the characters of the following species of Mammalia, which I believe have

\* It had escaped our attention till Mr. Howell's paper was already in type and our day of publication close at hand, that those of his observations which relate to the opposition of stigmata to placentæ in *Papaveraceæ*, and to the composition and cohesion of stigmata, had already been published by Mr. Brown in his account of the *Cyrtandraceæ* in Horsfield's ' Plantæ Javanicæ:' Mr. Howell appears not to have been aware of this fact.

In a subsequent number we shall be enabled to refer more fully to Mr. Brown's dissertation.